6. On the Methods of Feeding and the Mouth-parts of the Larva of the Glow-worm (*Lampyris noctiluca*). By Kathleen Haddon, Zoological Laboratory, Cambridge *.

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(Plate I.†)

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In many insects of widely separated groups digestion takes place partly outside the body, digestive fluids being exuded from the mouth upon or into the food, which is then sucked up in a liquid form. The mouth-parts are in some cases specially formed in connection with this habit, while in other cases there appear to be no peculiar modifications.

One type of modification seen in a few forms is that in which the mandibles are either grooved or pierced by a fine tube, and in which the groove or tube is the channel of egress for the digestive fluid, although there seems to be no clear evidence of this, except perhaps in the case of the Dytiscid larvæ: such modification is apparently found only in insects which feed chiefly or entirely upon the juices of their prey.

The glow-worm larva is one of those forms in which the mandibles are pierced by a fine tube, and as it feeds upon snails and slugs and leaves no residue, excepting the slime of its prey, Mr. F. Balfour-Browne suggested that I should study the mouth-parts to ascertain whether the food was eaten or sucked up.

A certain amount of spirit-material was available for dissection, but we were fortunate in obtaining a number of nearly full-grown living specimens at Wicken Fen in May.

Specimens required for section-cutting were first softened for about forty-eight hours in Perenyi's fluid, dehydrated, cleared in cedar-wood oil, and embedded in paraffin in the usual way. The sections were cut 8 μ thick and stained on the slide, first with eosin in ninety per cent. alcohol, then with picro-nigrosin in water.

External Features and Habits.

The larvæ were kept in an inverted bell-jar nearly filled with moist earth, and supplied with some moss. They were caught on May 14th, and for about a week were fairly active and ready to eat; but subsequently they became torpid, refused their food, and finally began to pupate—by June 1st all had pupated.

* Communicated by Frank Balfour-Browne, M.A. (Oxon. et Cantab.), F.R.S.E., F.Z.S.

† For explanation of the Plate see p. 82.

The habits of these larvæ have already been described by Newport * and later writers, but their accounts do not entirely agree. Newport describes the bite of the larva as causing great pain to the snails on which they feed; whereas Fabre †, in a popular article on the subject, says that the snail is anæsthetised by the bite. It may be of interest, therefore, to record my own observations, which were carried out with a Zeiss binocular, the larvæ being placed with some moss in a shallow glass dish and supplied with small snails.

The larvæ crawl about, feeling their way with their maxillary palps, which are kept constantly in motion, the head being fully extended, so that the whole of it protrudes beyond the prothorax; whereas when the animal is at rest only the mouth-parts are visible. The snail apparently is found quite by chance, and if hungry the larva at once fastens on its prey. The mandibles are worked laterally, and bending its head down it cuts its way into the snail, which promptly withdraws into its shell, the larva following. If left undisturbed the larva feeds continuously, and is frequently joined by others, until the snail is finished; but if it is pulled off at once, the snail pursues its way apparently uninjured. Wishing to see more clearly the method of procedure, I supplied small slugs as food instead of snails, so that there could be no retreat into a shell. The larva bit the slug on the visceral hump, but apparently could not get a sufficient hold, as the slug with a twist of its body slipped away leaving a mass of mucus over the head of its enemy. The larva at once desisted from its attack and tried to free itself from the slime by working its jaws and rubbing them with its front legs. These methods failing, it curled up and cleaned itself with the adhesive organs in the terminal portion of its abdomen, repeating the process long after there were any signs of slime on the head, probably to cleanse the hairy bases of the mouth-parts.

In the next attempt to feed the larvæ with slugs the attack was more fortunate, the larva striking right into the pulmonary cavity of its victim; but either the food was not to its taste or else it was not hungry, as it shortly let go, and the slug, which had previously been lethargic, glided off apparently undisturbed.

These observations show that—in these cases, at any rate—there was no anæsthetising.

When feeding, the larvæ keep their jaws constantly moving, and thus their mouth is bathed in the juices from the snail. Newport ‡ also observed some dark-coloured liquid, which flowed from the mouth of the larva at the time of its attack and apparently acted as a poison, for the snail was much more affected by the bite of a larva than by a mechanical injury, such as piercing with a needle. He apparently failed to notice that the mandibles

* G. Newport, "On the Natural History of the Glow-worm," Journal of the Proc. of the Linnean Society, Zoology, vol. i. 1857, p. 40.

† Fabre, "The Glow-worm," Century Magazine, November 1913.

‡ *Loc. cit.* p. 58.

of the larvæ are pierced by canals which communicate with the mouth, a fact described by Meinert* some time later. This observer suggested that the juices of the snail were sucked up through these tubes, the thick hairs which surround the mouth acting as a kind of absorbing sponge. More recently R. Vogel † has described these tubular mandibles, and he further asserts that he has seen the dark-coloured liquid mentioned by Newport flowing from them. As no salivary glands are to be found in this animal, he believes that the secretion originates in the mid-gut, as is said to be the case with the larva of *Dytiscus* and in *Carabus*.

Mouth-parts.

As stated above, the head of the *Lampyris* larva can be retracted within the prothorax, and in this position only the tips of the mouth-parts are visible. As the preserved specimens are usually in this position, the dorsal portion of the prothorax has to be cut away to expose the head (Pl. I. fig. 1). Only the mandibles are strongly chitinised; the first and second maxillæ are fleshy, their basal parts being distinguishable only by the sclerites (figs. 4 & 5). The labrum and hypopharynx are strengthened by chitin and covered with hairs.

Mandibles.

The mandibles (figs. 2, 3) are strong and much curved, and except at the distal end are covered with small hairs. There is a secondary tooth (*t.*) on the inner margin, which is sharply pointed on the right mandible and as a rule stouter and blunt on the left; in some cases, however, the left resembles the right.

The base of each mandible on the dorsal side is occupied by a thick brush of hairs, pointing towards the tip of the mandible. Along the inner edge, between the secondary tooth and the basal brush, there are longer and stiffer hairs than over the rest of the surface.

Along the outer border, and near the base, is a condyle (*c.*) for articulation with the labrum. Just inside this on the dorsal side is the posterior opening (*p.op.*) of the canal which pierces the mandibles; the anterior opening (*a.op.*) of this canal is on the outer margin of the mandible slightly to the side of the apex. Directly in front of the condyle is a group of short stout bristles.

Maxillæ and Labium.

These appendages (figs. 4 & 5) are fused posteriorly into a fleshy pad, and it is only ventrally that their component parts can be distinguished by means of the sclerites. Distally, however, the various parts of the appendages may easily be identified.

* F. Meinert, "Gjennemborede Kindbakke hos Lampyris og Dribus-Laverne," Ent. Tidskrift, vii. 1886.

† R. Vogel, "Beiträge zur Anatomie und Biologie der Larve von *Lampyris noctiluca*," Zool. Anz. xxxix. 1912, p. 515.

The maxillæ have on their ventral aspect a small square plate (*cd.*) representing the cardo, and a larger more elongated stipes (*st.*), which bears a few long bristles and some short flattened hairs. Externally is a stout four-jointed palp (*mx.p.*) with a few hairs, and internally a two-jointed palp-like galea (*ga.*) and a flat lacinia (*la.*), both covered profusely with hairs, the inner margin of the lacinia bearing a row of stiff bristles. Dorsally, the maxillæ have much the same appearance, except that the cardo is not represented and the stipes is small. At the base of the palp along the external border is a tuft of hairs pointing forward, as do all the hairs on these mouth-parts. Posterior to the tuft are a few more of the short flattened hairs, which are similar to those described by Packard * as taste-hairs.

The ventral view of the labium shows the transversely placed submentum (*sm.*) tapering from each end towards the middle. The mentum (*mt.*) is in the shape of an elongated triangle, the apex being anterior; it bears a few bristles and some short flattened hairs. Distally, there is a pair of short, fat, three-jointed palps (*la.p.*), with a few hairs.

Dorsally, there is a clump of hairs at the base of the palps, and another larger one more posteriorly.

Labrum.

The shape of the upper lip (fig. 6) is roughly trapezoidal, the anterior margin being the longest, and slightly indented in the middle. Posteriorly there is a deep bay, formed of a fork of chitin (*c.f.*) which protrudes beyond the rest of the labrum; the handle, as it were, of the fork forms the main support, or mid-rib (*mr.*), of the labrum, and bears two wing-like lateral expansions which keep the whole rigid.

Dorsally the surface is slightly rounded, but on the underside there is a mid-ventral ridge formed by the junction of the two sides, which slope steeply down towards it. There is on each antero-lateral corner a socket which receives the condyles on the mandible.

The whole of the ventral surface of the labrum is covered with numerous rows of tiny hairs, all of which point forwards. The rows themselves are arranged across the labrum, but slope forward from the sides towards the mid-ventral ridge. The anterior margin is beset with stiff bristles which bend slightly towards the middle.

The Hypopharynx.

The tongue, or hypopharynx (fig. 7), is in the shape of a triangle with the base bulged out; the apex is directed forwards, while at each end of the base is a chitinous knob (*art.*) articulating with a strut from the side of the head. With the exception of these knobs the hypopharynx is completely covered with hairs pointing forwards, as usual.

* A. S. Packard, 'Textbook of Entomology,' 1898, p. 282.

Viewed from the side, this organ is slightly curved upwards at the tip, and ventrally the surface is entire. On the dorsal side, however, there is a distinct groove (*gr.*) which fits the corresponding ridge on the labrum; the edge of the groove is strengthened by a thicker band of hairs. The hairs at the apex of the hypopharynx are longer than the others, and are frequently forked.

Interrelations of Mouth-parts.

The arrangement of the mouth-parts is such that it prevents any solid matter from entering the gullet. This is effected by the enormous number of hairs that surround the mouth, all pointing outwards, so that although the mouth is always open it is impossible for any solid particles to enter.

A comparison might be made here between this larva and the larva of *Dytiscus*, which also sucks the juices of its prey. The *Dytiscus* larva has its mandibles tubular, but the mouth can be closed by an apparatus which has been described as a "mouth lock," which automatically closes up the aperture when the mandibles shut. The larva pierces its prey with its mandibles, closes them, and proceeds to suck the juices through the mandible-tubes by means of the pharyngeal pump. When the mandibles open it can swallow small particles in the ordinary way *.

The Pharynx.

The floor and sides of the anterior end of the pharynx are strongly chitinised (fig. 8, *ph.*), and the tongue is a direct continuation of the floor. The sides at this point receive an additional support from the chitinous fork which protrudes from the posterior end of the labrum (fig. 6, *c.f.*). More posteriorly, the chitinous fork ends and the sides and floor of the pharynx become membranous, the chitin tapering down to a narrow ventral strip. The roof of the pharynx up to this point is also membranous, but here it turns sharply upwards and forms a small vertical chitinous plate (figs. 1 & 8, *c.p.*), from which muscles (fig. 8, *d.m.*) run to the dorsal integument of the head. From the apex of this plate another larger one slopes downwards (fig. 8, *c.p.'*), and runs into the dorsal surface of the œsophagus. Two strong bands of muscle (figs. 1 & 8, *p.m.*) are attached to the posterior surface of this plate, and run to the back of the larva's head; while from its edges bands of muscle (fig. 8, *l.m.*) run down on either side of the pharynx and are attached to the posterior end of the plate forming its floor. This plate is perforated by two pairs of small holes, the function of which I cannot ascertain at present.

This apparatus evidently forms a suction-pump, and is worked by contraction of the muscles attached to the two dorsal plates, which raises them and makes a vacuum into which the liquid food flows, while contraction of the lateral descending muscles

* L. C. Miall, 'The Natural History of Aquatic Insects,' 1912, p. 44.

lowers the roof again. A similar contrivance is found in some groups of Hemiptera*, only in them there are no ventral muscles, the roof falling back into its place by the natural elasticity of the pharynx.

The method of feeding of this larva is obviously different from that of the *Dytiscus* larva, for it has no means of shutting its mouth, and hence cannot suck through the mandible-tubes only. The mouth, although guarded by an immense number of outwardly directed bristles, has sufficient aperture to allow of the passage of a fine hair; this, if placed on the tip of the hypopharynx and pushed gently along, runs down into the pharynx. On the other hand, a hair pushed down the mandible-tube bends forwards and curves out again at the mouth; this is difficult to understand unless it is due to the forwardly directed hairs that lie on the base of the mandible. A stiffer bristle might overcome this resistance, but I could not insert one into the tube; it is probable that liquid, such as would be sucked up through the mandible, would trickle through the hairs and be drawn into the pharynx by the action of the suction-pump.

It is clear, at any rate, that no large particles of food can find their way through the mass of hairs that surround the mouth; they are are all strained off and removed later by the terminal adhesive organs. It is probably the difficulty of extracting these particles that causes the larva to continue to cleanse itself long after the apparent need for it is over.

EXPLANATION OF THE PLATE.

Lettering.

a.c., articulation for condyle of mandible; *ant.*, antenna; *a.op.*, anterior opening of canal through mandible; *art.*, articulation of hypopharynx; *br.*, brush of hairs on mandible; *c.*, condyle of mandible; *cd.*, cardo; *c.f.*, chitinous fork; *c.p.*, chitinous plate of pharynx; *c.p.'*, posterior chitinous plate; *d.m.*, dorsal pharyngeal muscle; *ga.*, galea; *gr.*, groove of hypopharynx; *hyp.*, hypopharynx; *la.*, lacinia; *lbr.*, labrum; *la.p.*, labial palp; *l.m.*, lateral pharyngeal muscle; *md.*, mandible; *m.r.*, mid-rib of labrum; *mt.*, mentum; *mx.p.*, maxillary palp; *œs.*, œsophagus; *op.*, opening into gullet; *ph.*, chitinous floor of pharynx; *p.m.*, posterior pharyngeal muscle; *p.op.*, posterior opening of canal through mandible; *pth.*, prothorax *sm.*, submentum; *st.*, stipes; *t.*, tooth on mandible.

The figures, with exception of fig. 8, were all drawn with a camera lucida.

Fig. 1. Dorsal view of the head of a larva (× 16). The prothorax has been cut away to expose it, and the dorsal integument removed.
2. Dorsal view of right mandible. (× 30.)
3. Dorsal view of left mandible. (× 30.)
4. Dorsal view of first maxillæ and labium (× 30). (Note asymmetrical sclerites.)
5. Ventral view of first maxillæ and labium. (× 30.)
6. Ventral view of labrum. (× 30.)
7. Dorsal view of hypopharynx. (× 30.)
8. Diagram of the pharyngeal pump.

* F. Muir and J. C. Kershaw, "On the Homologies of the Mouth-parts of Hemiptera," Psyche, vol. xviii. no. 1, 1911, p. 5.